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Home Range, Habitat Use and Survival of Coyotes in Western South Carolina

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Abstract.—Home range size, habitat use and survival of coyotes are variable throughout their range. Because coyotes have recently become established in South Carolina, we investigated their spatial distribution, habitat use and mortality on the Savannah River Site (SRS) in western South Carolina, USA. Annual survival for adult coyotes on the SRS was 0.658. Off-site trapping and shooting accounted for 60% of mortality. Home ranges averaged 30.5 km^2 and 31.85 km^2 by the 95% minimum convex polygon and 95% fixed kernel methods, respectively. We detected no difference in home ranges size between males and females. Intraspecific home range overlap averaged 22.4%, excluding mated pair interactions, with 87.5% of coyotes sharing their home range with one or more individuals. Coyotes selected home ranges containing higher proportions of early successional habitat than was available on the landscape. Core areas likewise contained a greater proportion of early successional habitat than available in the animal's home range.

Introduction

Coyotes (*Canis latrans*) are historically associated with western North America. However, during the last 50 y, they have expanded their range into the southeastern United States, aided largely by humans (Hill *et al.*, 1987). Moreover, coyote harvests have increased dramatically in Georgia and South Carolina in recent years (GADNR, SCDNR unpublished data). Coyote ecology has been intensively studied throughout much of its North American range, and this research has indicated a high degree of behavioral plasticity (Bekoff, 1977; Holzman *et al.*, 1992) which has been related to prey characteristics (Bowen, 1981) and habitat variables (Gese *et al.*, 1988). Because Southeastern ecosystems are inherently different than Southwestern ecosystems in availability of food items and habitat, additional study is necessary to understand differential coyote habits in these novel environments. We chose the Savannah River Site in west central South Carolina to study coyote survivorship, home range size and habitat use. Our objectives were to establish baseline numbers for

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similar coyote populations in the region and to provide information on coyote habits to aid in wildlife and habitat management decisions.

STUDY AREA AND METHODS

Research was conducted on the 78,000 ha Savannah River Site (SRS) in Aiken, Barnwell and Allendale counties, South Carolina, USA. The SRS is a U.S. Department of Energy National Environmental Research Park located in the Upper Coastal Plain physiographic province along the Savannah River (Imm and McLeod, 2005). Topography of the SRS is flat to gently rolling and elevation ranges from 20–130 m above sea level. Used primarily for agriculture until 1950, SRS is now predominately forested (97%). Longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pines dominated the forest canopy (68%). Other major vegetative suites include swamps and bottomland hardwood (22%) and upland hardwood (7%) forests (Imm and McLeod, 2005). Approximately 12% of the total forest stands were $<$10 y of age (Blake and Bonar, 2005). The SRS was intersected by over 2600 km of roads, logging trails and railroads (Blake *et al.*, 2005).

Coyotes were first reported on the SRS in 1986 and since that time, the population has expanded dramatically (Mayer *et al.*, 2005) and coyotes are now observed frequently, even during daylight hours. Although coyotes are subject to trapping during Jan. and Feb. and opportunistic shooting on adjacent private properties, they were not subject to persecution on SRS during the course of this study.

CAPTURE AND RADIO TELEMETRY

We captured coyotes with offset jawed #1.75 leghold traps (Woodstream Corp., Lititz, PA). Coyotes were anesthetized with 0.6 ml medetomidine (1.0 mg/ml; Domitor®, Novartis Animal Health Canada Inc., Mississauga, Ontario) delivered intramuscularly via a jab stick, followed by 0.3 ml at 15 min post initial injection as needed. Each animal was blindfolded, muzzled and evaluated for indications of age (Gier, 1968) and reproductive status. Animals estimated to be $\geq$1 y of age were ear tagged and fitted with a motion-sensitive radio-collar (200 g, 3.2 y battery life, ATS Telemetry, Inc., Isanti, MN) equipped with a mortality switch. Vital signs (heart rate, body temperature) were monitored during handling, blood and tissue samples collected, and animals weighed. Chemical immobilization was reversed using 0.6 ml atipamezole (5.0 mg/ml; Antisedan®, Novartis Animal Health Canada Inc., Mississauga, Ontario). Capture and handling procedures were approved by the University of Georgia (UGA) Institutional Animal Care and Use Committee; UGA Animal Welfare Assurance # A3437-01.

Radio tracking was conducted with point locations from Jun. 2005 through Jul. 2006. Radio monitoring for survival continued through Sept. 2006. We estimated locations of coyotes via biangulation and triangulation from 2–5 telemetry bearings using handheld Yagi antennas. Only bearings taken within a 20 min interval were used for the estimation of locations to decrease error associated with animal movements. In the case of biangulations, we limited the inter-bearing angle to $>50^\circ$ and $<130^\circ$ to minimize error. Average ($\pm$SE) location error distance (Zimmerman and Powell, 1995) estimated from 24 test collars placed 126–1281 m away from observers at unknown locations was 124 m ($\pm$21.3), with an average angular error of $11 \pm 1.3^\circ$. Our realized error may have been somewhat larger due to potential animal movements between subsequent locations. Locations were estimated using the Andrews-M estimator in the computer program L.O.A.S. (Ecological Software Solutions, Inc., Sacramento, CA). Triangulations resulting in an error ellipse area $\geq$4 ha were discarded. We attempted to locate each individual 1–2 times a week and distributed

Table 1.—Name, number of parameters (*K*), and description of AIC_c models used in estimation of coyote survival on the Savannah River Site, SC

Model	*K*	Description
Constant	1	Overall survival with no effect of sex or time
Sex	2	Differential male and female survival
Seasonal, constant	6	Time grouped by 2 month seasons (Jan + Feb, Mar + Apr, etc)
Seasonal, year effect	10	Time grouped by 2 month seasons, but considers 2005 separately from 2006
Month	18	18 months considered individually
Sex X Month	36	18 months considered individually with differential male and female survival

tracking events systematically throughout the diel period. Successive locations were separated by a minimum of 12 h and assumed to be independent (Reynolds and Laundre, 1990).

SURVIVAL

We used the known-fate model in the program MARK (Version 4.3) to estimate survival of radio marked individuals. The known fate procedure allowed for staggered entry of coyotes throughout the capture period. We assumed that our sample was representative of the population, capture and marking had no effect on survival, and time of capture was independent of survival. We constructed models based on sex, month, season and year to determine factors affecting coyote survival (Table 1). Akaike's Information Criteria (AIC; Akaike, 1973; Burnham and Anderson, 2002) was used to select the best-fit model. In two of the survival models we grouped months into the following 2 mo seasons corresponding with biological and anthropogenic factors likely to affect coyote survival: Jan.–Feb., breeding and trapping season; Mar.–Apr., gestation; May–Jun., nursing; Jul.–Aug., weaning; Sept.–Oct., pup independence; Nov.–Dec., pre-breeding and SRS deer hunts. We also present annual survival estimates using the Kaplan-Meier approach adjusted for staggered entry (Pollock *et al.*, 1989).

HOME RANGE

We estimated individual annual home ranges for coyotes with ≥30 telemetry locations (Seaman *et al.*, 1999) with 95% fixed kernel (FK; Worton, 1989) and 50% FK isopleths using Home Range Tools (Rodgers *et al.*, 2005) for ArcGIS 9 (Environmental Systems Research Institute, Inc., Redlands, CA). We used least squares cross-validation (LSCVh) to select the kernel smoothing factor (Seaman *et al.*, 1999).

We also report 95% minimum convex polygon (MCP) home ranges using Home Range Tools (Rodgers *et al.*, 2005) for ArcGIS 9 (Environmental Systems Research Institute, Inc., Redlands, CA) because this method has been used most consistently in previous studies (Holzman *et al.*, 1992). To determine the minimum number of locations needed to estimate MCP home ranges, we used the Animal Movements Extension 2.1 (Hooge and Eichenlaub, 2000) in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA) to calculate 100 bootstrap estimates of MCP home range area using 10-all randomly selected locations for all coyotes. We plotted the mean MCP area by the number of locations (area-observation curve) used in the bootstrap re-sampling and used the number of locations at which the area increased by <1% with the inclusion of an additional location as the minimum number of locations

Table 2.—Habitat types available on the Savannah River Site, SC used in compositional analysis and simplified rankings of habitat selections by coyotes from June 2005 - July 2006 based on a modification of Johnson's (1980) selection orders (see Methods for details). Higher numbers indicate selection

Habitat	Area (ha)	Description	Rank	
			Second order	Third order
Water	1735	Open water, lakes, ponds, rivers	1	2
Young Pine	6218	Pine stands 5-15 years old	4	1
Middle Pine	10397	Pine stands 16-30 years old	5	3
Mature Pine	30109	Pine stands >30 years old	3	5
Hardwood	24342	Hardwood and mixed forests stands >15 years old	2	4
Early Successional	7539	Grass, brush, hardwood stands <10, pine stands <5	6	6

needed to calculate 95% MCP home range (Odum and Kuenzler, 1955). We compared home range estimates between males and females using Student's t test (PROC TTEST, SAS).

We calculated the percent of home range overlap for coyotes with adjacent home ranges at both the 95% FK and 50% FK levels. We used ArcGIS 9 (Environmental Systems Research Institute, Inc., Redlands, CA) to overlay coyote home range projections and calculate the area of overlap. The percent overlap was calculated by dividing the area of overlap by the total area of the coyote's home range or core area. Interactions between mated pairs were considered separately. We defined mated pairs as an adult male and adult female coyote commonly located (>10% of locations) in close proximity (<100 m) of each other. This close proximity was very rare among other individuals. We present the mean overlap for individuals sharing part of their home range with more than one other coyote. In overlap calculation, we excluded transient individuals and individuals not surviving for >10 mo of the study.

HABITAT SELECTION

We developed a GIS-based habitat map for the SRS based on the U.S. Forest Service FSVEG database and stands coverage (U.S. Forest Service, unpublished data) using ArcGIS 9 (Environmental Systems Research Institute, Inc., Redlands, CA). We delineated six habitats based on forest stand species composition and age (Table 2) and calculated the proportions of each habitat within each coyote's 95% FK and 50% FK overlap.

We defined habitat selection on two levels according to a modification of Johnson (1980). Second order selection refers to habitats available within the home range versus general availability across the study area. We defined third order selection as the habitat use within the core area versus habitat availability within a home range. We defined study area, home range and core area as the entire SRS, the 95% FK isopleth, and the 50% FK isopleth for each animal, respectively.

We used compositional analysis (Aebischer *et al.*, 1993) to examine habitat selection. Habitat use and availability proportions were compared using multivariate analysis of variance (MANOVA) with BYCOMP.SAS (Ott and Hovey, 1997) for both orders of selection. Habitat use and availability proportions for coyotes believed to be mated pairs (based on observations of male/female interactions and shared home ranges) were combined to avoid pseudoreplication (Thornton *et al.*, 2004). BYCOMP.SAS generates a Wilks' Lambda statistic and associated F-value for overall use versus availability. In addition, matrices of t tests were

Table 3.—Candidate models, number of parameters (*K*), Akaike's Information Criterion with the small-sample bias adjustment, Δ AICc, and Akaike weights for predicting coyote survival on the Savannah River Site, SC, April 2005-September 2006

Model	*K*	AIC_c	Δ AIC_c	AIC_c Weights
Seasonal, constant	6	125.71	0.000	0.958
Seasonal, year effect	10	131.99	6.284	0.041
Constant	1	142.04	16.332	0.000
Sex	2	144.02	18.315	0.000
Month	18	144.54	18.827	0.000
Sex X Month	36	179.97	54.258	0.000

constructed to examine preferences between each pair of habitat types (Aebischer *et al.*, 1993).

RESULTS

Between Apr. and Oct. 2005 we captured 33 adult (14 female, 19 male) and 7 juvenile (<1 y old) coyotes. Adult males (13.53 ± 0.51 kg) weighed more (t = −2.49, P = 0.017) than adult females (11.67 ± 0.53 kg). We recorded 1603 locations between Jun. 2005 and Jul. 2006 from radio telemetry (75% biangulations) and an additional 36 locations from visual sightings. Locations were dispersed throughout the diel period as follows: 2400-0800, 20%; 0800–1600, 42%; 1600–2400, 38%. We lost contact or had only sporadic contact with five of the 33 coyotes we collared, suggesting that these animals were transients or had made an atypical excursion onto our study area at the time of capture.

We used 33 adult coyotes (14 female, 19 male) monitored from Apr. 2005 through Sept. 2006 to estimate survival. Of the 10 known coyote mortalities, four animals were trapped outside of the study area, two were shot on adjacent properties, two deaths were associated with heartworm infestation and two were of unknown causes. In both unknown cases, the coyote was in an advanced stage of decomposition at time of recovery. Five animals were censored following the last day of radio contact. We recovered only the radio collar of one animal which was also censored.

Annual survival for adult coyotes on the SRS was 0.658 (CI = 0.480–0.836). Of the six survival models, the model ''Seasonal, constant'' received 0.958 of the AIC_c weight, which was >23 times more than the second best model ''Seasonal, annual'' (Table 3).

Based on bootstrap estimates, 18 coyotes (8 female, 10 male) had sufficient locations ($\bar{x}$ = 35, range 30–62) to calculate 95% MCP home ranges. MCP home ranges averaged 30.5 (±8.6) km^2 (range 3.7–137.0 km^2; Table 4). We also calculated 95% MCP home ranges with the removal of one male and one female that could be considered transients due to home ranges of 82 km^2 and 137 km^2, respectively. MCP home range with removal of transients averaged 20.61 (±5.4) km^2 and we detected no difference (t_{14} = −0.76, P = 0.46) between the sexes.

Sufficient locations (>30) were collected to calculate FK home ranges for 22 coyotes (10 female, 12 male). Overall 95% FK isopleths averaged 31.85 (±8.3) km^2 (range 4.2–147.9 km^2) and 50% FK isopleths averaged 6.73 (±1.7) km^2 (range 0.62–33.6 km^2; Table 4). With the removal of transients, 95% FK and 50% FK home ranges averaged 24.25 (±4.7) and 5.42 (±1.1) km^2, respectively. We detected no difference in 95% FK (t_{18} = −1.35, P = 0.192) and 50% FK (t_{18} = −1.52, P = 0.145) home ranges between the sexes.

Table 4.—Sex, number of radio locations (n), home range sizes, and percent overlap of home ranges and core areas of adult coyotes on the Savannah River Site, SC from June 2005-July 2006

			95% Fixed Kernel				50% Fixed Kernel		
Sex	n	MCP (ha)	home range (ha)	overlap[a]	overlaps with[a]	mated pair overlap	core area (ha)	overlap	overlaps with
Female	83	876	1371	96.2%	1 M		333	69.7%	M
Female[c]	77	374	425	34.0%	2 F, 2 M	75.5%	62	92.9%	Male[c]
Female	76	520	811	21.1%	1 F, 3 M		179	1.7%	M
Female	91	1418	1419	17.0%	2 F,5 M		164	0.0%	none
Female[b]	92	5218	3198	5.9%	2 F, 2 M	78.6%	609	77.3%	Male[b]
Female[d]	58	1612	2167	0.0%	none	90.5%	461	88.0%	Male[d]
Female	58[e]	1598	2159	0.0%	none		515	0.0%	none
Female[g]	49	1147	1801				402		
Female[f]	51	13709	14793				3365		
Female[g]	45[e]	1266	2340				572		
Male	85	1346	2193	60.2%	1 F		652	35.6%	F
Male[c]	86	496	468	44.3%	1 F, 2 M	68.6%	71	81.0%	Female[c]
Male	95	758	1042	42.9%	1 F, 1 M		238	65.1%	M
Male	86	1191	1634	13.8%	4 F, 3 M		354	0.0%	none
Male	63	1296	2187	8.2%	3 F, 3 M		668	0.0%	none
Male	75	4577	5361	6.2%	2 F, 2 M		1172	13.2%, 0.3%	M, F
Male[d]	74	3120	2622	4.0%	2 M	74.8%	585	69.4%	Female[d]
Male[b]	57	8086	5118	3.6%	2 M	49.1%	1001	47.0%	Female[b]
Male	89	954	1502	1.4%	1 M		353	0.0%	none
Male[g]	31[e]	5865	9378				2196		
Male[f]	62	8207	10246				1608		
Male[g]	30[e]	690	1317				254		

[a] Excludes mated pair overlap.
[b,c,d] Letters correspond with mated pairs.
[e] Bootstrap resampling indicates insufficient locations for 95% MCP.
[f] Transient excluded from overlap due to overlap with ≥10 individuals.
[g] Excluded from overlap due to mortality.

Of the 22 coyotes for which FK home ranges were calculated, 16 met our criteria for home range overlap analysis. Fourteen of these coyotes (87.5%) had 95% FK home ranges that overlapped with the 95% FK home ranges of one or more other individuals. Excluding mated pair interactions, 95% FK overlap averaged 22.4% (±6.7). Six coyotes (3 male, 3 female) were believed to be mated pairs based on telemetry locations and observations. Mated pair overlaps averaged 72.9% (±5.6) for 95% FK home ranges and 75.9% (±6.7) for 50% FK core areas. Five coyotes (2 female, 3 male) that were not part of a known mated pair had overlaps of the 50% FK core area with one or more other individuals that averaged 18.5% (±8.8) (Table 4). We detected no difference in the average percent overlap between unmated males and females at the 95% FK home range ($t_{14} = 0.31$, $P = 0.760$) or the 50% FK core area ($t_8 = -0.06$, $P = 0.955$).

Compositional analysis indicated that habitat use differed from availability at both the second order ($F_{[5, 14]} = 15.51$, $P = 0.0001$) and third order ($F_{[5,14]} = 3.89$, $P = 0.019$) level for coyotes on the SRS. Coyotes selected home ranges (second order) with early successional habitat over mature pine stands ($t_{18} = 2.54$, $P = 0.019$), hardwood stands ($t_{18} = 2.72$, $P = 0.013$), young pines ($t_{18} = 1.93$, $P = 0.078$) and middle-aged pines ($t_{18} = 1.97$, $P = 0.062$). Coyotes selected core areas (third order) with early successional habitat over young pines ($t_{18} = -2.05$, $P = 0.008$) and mature pines over young pines ($t_{18} = -1.66$, $P = 0.088$). Simplified ranks based on observed t statistics and randomized p-values are presented in Table 2.

DISCUSSION

Throughout much of the range of coyotes, anthropogenic factors account for the majority of mortality (Andelt, 1985; Tzilkowski, 1980; Roy and Dorrance, 1985; Chamberlain and Leopold, 2001). Our results confirm this for southeastern coyotes with 60% of mortality attributable to shooting (n = 2) and trapping (n = 4) despite these activities not occurring within the boundary of the SRS and the best-fit survival model grouped Jan. and Feb. (trapping season) which accounted for 40% of the total mortality. However, our results are based on only 15 mo of observation and may not be indicative of long term trends. Chamberlain and Leopold (2001) reported similar survival ($S = 0.733$ during 1993–1997) for adult coyotes in their study area in Mississippi. They concluded that harvest by sport hunters was the primary mortality factor affecting southeastern coyote populations and that trapping was having little effect due to low fur prices. Like the SRS, no trapping occurred on their study area, but sport hunting was permitted.

Trappers that captured our study animals off-site reported they planned to sell the animals live to fox pens. Fox pens are large enclosures in which foxes (or coyotes) are pursued with hounds for sport. Based on this study, trapping may impact local southeastern coyote populations, particularly in states that tolerate the live sale of coyotes.

Variation in coyote home range size is evident across North America (Gipson and Sealander, 1972; Andelt and Gipson, 1979; Gese *et al.*, 1989; Holzman *et al.*, 1992) and is influenced by habitat composition (Gese *et al.*, 1988). Based on this, coyote home ranges should be comparable within the same geographic region given similar habitats. Coyotes on SRS had larger home ranges than those reported for Mississippi (14.8 km^2, Chamberlain *et al.*, 2000), Georgia (10.1 km^2, Holzman *et al.*, 1992), and Florida (24.8 km^2, Thornton *et al.*, 2004). Wooding (1984) and Sumner (1984) each reported home ranges of 27.0 km^2 and 33.4 km^2, respectively, for coyotes in Alabama and Mississippi. These two studies present home range sizes most similar to our findings, but they are based on sample sizes of six (Wooding, 1984) and seven (Sumner, 1984) coyotes. Thornton *et al.* (2004) based their home range estimation on seven coyotes. In addition to the possible bias associated with small sample size, there is difficulty in comparing home range sizes of coyotes among studies due to differences in sampling methods (Laundre and Keller, 1984) and different home range estimators (Woodruff and Keller, 1982). Based on our data, the inclusion or exclusion of transients, and the means at which transients are defined can also impact the average home range size of coyotes. If we include two animals that we defined as transients, our results present the largest documented home ranges of coyotes in the Southeast. Exclusion of these two animals still produces home range estimates larger than those from Georgia and Mississippi. Holzman *et al.* (1992) speculated coyote home ranges may increase in size with an increasing proportion of forested habitat. Given the forested composition of the SRS, our data support this suggestion.

Holzman *et al.* (1992) and Chamberlain *et al.* (2000) reported larger home ranges for adult female coyotes than males. We detected no differences in home range size between the sexes. Our findings are in agreement with those of Laundre and Keller (1984) who standardized and compared the results of several studies and found no evidence of differential home range size between males and females.

Previous southeastern studies have found little overlap in home range and core areas between neighboring coyotes with the exception of mated pair interactions (Chamberlain *et al.*, 2000; Thornton *et al.*, 2004). However, our data suggests there is wide variation in the amount of intraspecific overlap at both the home range and core area level. In fact, our observed overlap should be considered a minimum because non-collared coyotes were seen in the home ranges of marked animals. Camenzind (1978) proposed that four social organizational classes of coyotes existed on the National Elk Refuge in Jackson, WY ranging from single nomad coyotes to packs. Coyote social group size may be correlated with prey size (Bowen, 1981). Coyotes on SRS do not often prey on large mammals (Schrecengost *et al.*, 2008) or defend carrion as a group resource (Schrecengost, unpublished data) so there is little evident competitive advantage in pack formation. However, we believe a gradient of social organization exists in southeastern coyote populations evident by the wide range of home range overlap although well defined group associations appear to be rare at SRS.

The broad geographic range of coyotes throughout North America is evidence of their ability to adapt and thrive in different habitats. However, within a suite of habitats coyotes may exhibit preference for certain types (Gese *et al.*, 1988). Although habitats on the SRS are fragmented, coyotes consistently chose home ranges and core areas with higher proportions of early successional habitat than were available on the landscape. Coyotes have been shown to prefer habitats with high prey abundance (Litvaitis and Shaw, 1980; Gese *et al.*, 1988; Chamberlain *et al.*, 2000) and coyotes in Georgia regularly used early successional habitats for nocturnal foraging areas (Holzman *et al.*, 1992). The preference of early successional habitats by coyotes on SRS is likely associated with high dietary use of soft mast species such as *Prunus* spp., *Rubus* spp. and *Phytolacca* sp. (Schrecengost *et al.*, 2008). Holzman *et al.* (1992) proposed coyotes may select mature pine stands due to availability of den sites, consistent with our data because mature pines ranked second in preference at the core area level.

MANAGEMENT IMPLICATIONS

This study presents further evidence of the variability associated with coyote spatial patterns and emphasizes the limitations of local studies for drawing conclusions about coyote behavior on a regional level. However, when combined with previous research, reasonable expectations can be formed pertaining to coyote populations throughout the southeastern United States. Coyotes on the Savannah River Site had larger home ranges with more intraspecific overlap than has been reported elsewhere in the southeastern United States. The efficacy of lethal coyote control has been associated with the presence of transient individuals (Windberg and Knowlton, 1988; Holzman *et al.*, 1992). In south-central Georgia, Holzman *et al.*, (1992) classified two of 17 coyotes as transients, similar to the proportion of transients in our South Carolina sample, and suggested that local coyote control may be effective. Despite no exploitation of coyotes on the 78,000 ha SRS, anthropogenic causes accounted for most mortality. This, along with the large home range size suggests that lethal coyote control efforts may need to be extensive as well as intensive to effectively reduce coyote use of a given area.

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